PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Influence of shade tolerance and development stage on the allometry of ten temperate tree species

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Abstract Allometry studies the change in scale between two dimensions of an organism. The metabolic theory of ecology predicts invariant allometric scaling exponents, while empirical studies evidenced inter- and intra-specific variations. This work aimed at identifying the sources of variations of the allometric exponents at both inter- and intra-specific levels using stem analysis from 9,363 trees for ten Eastern Canada species with a large shade-tolerance gradient. Specifically, the yearly allometric exponents, $\alpha_{v,\text{DBH}}$ [volume (v) and diameter at breast height (DBH)], $\beta_{v,h}$ [v and height (h)], and $\gamma_{h,\text{DBH}}$ (h and DBH) were modelled as a function of tree age for each species. $\alpha_{v,\text{DBH}}$, and $\gamma_{h,\text{DBH}}$ increased with tree age and then reached a plateau ranging from 2.45 to 3.12 for $\alpha_{v,\text{DBH}}$, and 0.874–1.48 for $\gamma_{h,\text{DBH}}$. Pine species presented a local maximum. No effect of tree age on $\beta_{v,h}$ was found for conifers, while it increased until a plateau ranging from 3.71 to 5.16 for broadleaves. The influence of shade tolerance on the growth trajectories was then explored. In the juvenile stage, $\alpha_{v,\text{DBH}}$, and $\gamma_{h,\text{DBH}}$ increased with shade tolerance while $\beta_{v,h}$ was shade-tolerance independent. In the mature stage, $\beta_{v,h}$ increased with shade tolerance, whereas $\gamma_{h,\text{DBH}}$ decreased and $\alpha_{v,\text{DBH}}$ was shade-tolerance independent. The interaction between development stage and shade tolerance for allometric exponents demonstrates the importance of the changing

functional requirements of trees for resource allocation at both the inter- and intra-specific level. These results indicate the need to also integrate specific functional traits, growth strategies and allocation, in allometric theoretical frameworks.

Introduction

Allometry studies the change in scale between two dimensions of a considered organism. This is generally expressed through the following equation (Eq. 1) between the dimensions Y and X:

$$Y = m \cdot X^{\mu_{y,x}} \tag{1}$$

The parameter m is a normalization constant which was found to depend on the size of an organism (Gillooly et al. 2001). The allometric exponent, $\mu_{y,x}$, is mostly considered as constant. In vascular plants, the allometric exponents, $\alpha_{v,\text{DBH}}$ [$Y = $ volume (v) and $X = $ diameter at breast height (DBH)], $\beta_{v,h}$ [$Y = v$ and $X = $ height (h)] and $\gamma_{h,\text{DBH}}$ ($Y = h$ and $X = \text{DBH}$) are of particular interest since they can provide information about how trees allocate their resources (Pretzsch et al. 2012). Equation 1 can be rearranged to express the relative change in Y versus the relative change in X (Eq. 2). Therefore, a variation of 1 % in X during a growth year i induces a variation of $\mu_{y,x}$ % in Y during a growth year i:

$$\mu_{y,x_i} = \frac{\mathrm{d}Y_i}{Y_i} \left/ \frac{\mathrm{d}X_i}{X_i} \right. \tag{2}$$

The metabolic scaling theory (MST) predicts the allometric exponent value by taking into account the structure

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and functioning of organisms (West et al. 1997). This theory considers that the plant vascular system can be assimilated to a "fractal-like network" and states that $\mu_{y,x}$ should scale with multiples of ¼ (West et al. 1999, 2009).

A large number of studies focused on improving the MST, as it provides a large panel of predictions, in order to understand the functioning of plants and forest ecosystems (Enquist et al. 2009; West et al. 2009). However, empirical results have shown that allometric exponents may not be invariant (Deng et al. 2008; Duursma et al. 2010). Work is still needed to explain these deviations from the theory (Price et al. 2012) and to adjust the MST according to empirical observations (Niklas 2004; Price et al. 2012).

Firstly, the allometric exponents have been shown to have intra-specific variations. Indeed, in *Fagus sylvatica* growing in Europe, the allometry between biomass and DBH or tree height has been demonstrated to vary with tree age (Genet et al. 2011). Moreover, it has also been established that $\alpha_{v,\mathrm{DBH}}$, $\beta_{v,h}$ and $\gamma_{h,\mathrm{DBH}}$ are not constant for three European temperate species and may vary with the development stage (Pretzsch et al. 2012). A lot of work has been carried out on the relationship between height and DBH (Henry and Aarssen 1999; Watt and Kirschbaum 2011; Lines et al. 2012), while the allometry between volume and DBH or volume and height has been less studied (Pretzsch et al. 2012). By considering the three allometries simultaneously, inferences regards allocation strategies can be made. In addition, species' trajectories of allometric exponents as a function of development stage have not been clearly established.

Secondly, inter-specific allometric exponent differences have also been observed. The allometric exponent between foliage biomass and crown woody biomass was found to be significantly different between 17 temperate gymnosperm species (Duursma et al. 2010). The allometry representing the self-thinning law of forests for 11 European and Mediterranean species was also found to be species dependent (Charru et al. 2012). A large variation in $\alpha_{v,\mathrm{DBH}}$ and $\gamma_{h,\mathrm{DBH}}$ was observed across 52 temperate species, while no results have been reported for $\beta_{v,h}$ (Pretzsch and Dieler 2012).

The three allometric exponents considered could be understood as an investment of trees in the different compartments (Eq. 2). Indeed, this formulation can be interpreted as the choice of a tree to allocate resources to volume, height or DBH growth, which also represents how trees fill their functional requirements. It is known that the functional requirements of trees differ: (1) at the intra-specific level with changes between the juvenile and mature stages (Lachenbruch et al. 2011), or (2) at the inter-specific level according species functional traits (Violle et al. 2007). However the impact of such requirements and variations of compartment allocation on tree allometry is not well understood.

We considered the variability in allometric exponents as a fact (Price et al. 2012; Pretzsch and Dieler 2012) and rather than confirming or invalidating the MST, we aimed at identifying some of the sources of variation of the allometric exponents in order to propose a framework that would improve the formulation of the MST. Therefore, the objectives of our work were twofold: we aimed at establishing the inter- and intra-specific variations in $\alpha_{v,\mathrm{DBH}}$, $\beta_{v,h}$ and $\gamma_{h,\mathrm{DBH}}$. Our hypothesis was that investment in height compared to diameter decreased with development stage such that $\alpha_{v,\mathrm{DBH}}$ should increase with tree age whereas $\beta_{v,h}$ and $\gamma_{h,\mathrm{DBH}}$ should decrease with tree age. We then explored the relationship between variations with development stage and shade tolerance. Shade tolerance is a functional trait that conditions the way that trees will allocate their resource under a given light condition (Canham 1988; Givnish 1988; Valladares and Niinemets 2008). This functional trait is particularly adapted in the study of $\alpha_{v,\mathrm{DBH}}$, $\beta_{v,h}$ and $\gamma_{h,\mathrm{DBH}}$ since these allometric exponents represent the growth investment of trees in primary and secondary growth. As has been previously suggested for $\gamma_{h,\mathrm{DBH}}$ and $\alpha_{v,\mathrm{DBH}}$ (Pretzsch and Dieler 2012), we hypothesized that shade tolerance explains the inter-specific variation in allometric exponent.

Materials and methods

Study area and data collection

Stem analysis data were collected by the Forest Surveys Branch of the Quebec Ministry of Natural Resources (MRNF 2009). A total of 9,363 stem analyses obtained between 2000 and 2006 were available for ten common species in the managed forest of Québec: *Abies balsamea* (balsam fir), *Betula papyrifera* (paper birch), *Picea glauca* (white spruce), *Picea mariana* (black spruce), *Picea rubens* (red spruce), *Pinus banksiana* (jack pine), *Pinus strobus* (eastern white pine), *Populus grandidentata* (big tooth aspen), *Populus tremuloides* (trembling aspen) and *Thuja occidentalis* (eastern white cedar).

The sampling design was established such that most of the ecological regions of Quebec were sampled. The randomly selected forest stands where the plots were placed were naturally regenerated and unmanaged. Between five and ten dominant and co-dominant trees per plot were felled. On each tree, disks were sampled at 0.15, 0.6, 1, 1.3, 3 m and every 2 m upward until the top of the tree. A complete description of the sampling design is available in Schneider et al. (2013). The characteristics of the sampled trees are given in Table 1.

Table 1 Data set statistics (SDs *in parentheses*)

Species	No. trees	Tree age (years)	Span of tree age (years)	DBH (cm)	Tree height (*h*; m)	Aboveground volume (*v*; dm^3)	Shade tolerance[a]	$\alpha_{v,\mathrm{DBH}}$	$\beta_{v,h}$	$\gamma_{h,\mathrm{DBH}}$
Abies balsamea	2,588	88 (28)	30–235	19.8 (4.4)	16.7 (2.9)	299 (161)	3	2.50 (0.73)	2.89 (1.55)	1.08 (0.93)
Betula papyrifera	640	73 (14)	37–125	17.1 (4.2)	17.4 (2.4)	239 (146)	7	2.53 (0.71)	3.48 (2.23)	0.94 (0.95)
Picea glauca	1,267	91 (27)	36–317	25.9 (6.3)	18.8 (3.5)	587 (356)	4	2.42 (0.66)	3.12 (1.67)	1.00 (0.85)
Picea mariana	2,736	96 (31)	45–262	17.0 (3.9)	15.7 (2.8)	210 (121)	4	2.48 (0.67)	2.76 (1.22)	1.04 (0.69)
Picea rubens	96	89 (27)	64–191	22.5 (3.5)	17.9 (1.7)	410 (150)	4	2.68 (0.82)	3.10 (1.14)	1.00 (0.68)
Pinus banksiana	941	85 (18)	33–157	18.5 (5.6)	16.7 (3.3)	295 (217)	9	2.81 (0.97)	2.98 (1.99)	1.18 (0.78)
Pinus strobus	48	100 (25)	44–142	35.9 (9.2)	25.5 (4.7)	1580 (891)	6	2.70 (0.69)	3.26 (1.47)	1.06 (0.79)
Populus grandiden-tata	183	70 (16)	44–122	27.0 (4.9)	25.2 (3.2)	813 (374)	9	2.57 (0.56)	4.16 (2.45)	0.79 (0.62)
Populus tremuloides	721	70 (15)	32–127	24.9 (5.1)	22.4 (2.9)	650 (311)	9	2.60 (0.60)	4.00 (3.96)	0.83 (0.71)
Thuja occidentalis	143	132 (46)	54–286	22.8 (7.2)	13.8 (2.3)	337 (234)	3	2.20 (0.53)	3.46 (1.64)	0.74 (0.37)
Total	9,363	89 (29)	30–317	20.2 (5.9)	17.4 (3.7)	353 (290)	–	2.52 (0.73)	3.04 (1.90)	1.03 (0.81)

DBH diameter at breast height

[a] Shade tolerance extracted from Humbert et al. (2007)

Computation of allometric exponents

From each disk, rings were counted and ring width measured using Windendro on four perpendicular radii on each disk below 1.3 m and on two opposite radii for disks higher than 3 m. Then ring-width chronologies were cross dated using COFECHA software (Holmes 1983) and averaged in order to have one ring width per year for each disk.

Past height growth was estimated by interpolation (Carmean 1972; Newberry 1991). Annual volume increment was obtained by estimating the volume of each section bounded by two successive disks (stem frustum) using Smalian's formula (Loetsch et al. 1973). This method, based on yearly disk diameters obtained from the ring-width measurements, considers that the stem frustum is a paraboloid. Total stem volume is obtained by summing the stem frustum volumes. Branch volume was estimated by using biomass equations developed for the most common species in Canada (Lambert et al. 2005) in combination with average species wood densities obtained from the Dryad data repository (Chave et al. 2009). The total aboveground volume (i.e. stem + branch volume) was then obtained by summing the stem and branch volumes. Hereafter, we considered only the aboveground volume as it is more meaningful for tree function and structure. All analyses were previously performed using the stem volume and led to the same results.

Total height, DBH, and the aboveground volume of each tree for each year were thus available. The yearly allometric exponents $\alpha_{v,\mathrm{DBH}}$, $\beta_{v,h}$ or $\gamma_{h,\mathrm{DBH}}$ were finally computed using Eq. 2.

Model construction

As a first step, we built models to express the allometric exponents as a function of tree age. Tree age was set from the first cross-section of each tree and therefore corresponded to the age of the tree determined at a height of 0.15 m.

Through visual analysis of the data, we observed that $\alpha_{v,\mathrm{DBH}}$ increased with tree age to reach a horizontal asymptote for most species while *Pinus* species seemed to reach a local maximum and then their $\alpha_{v,\mathrm{DBH}}$ decreased (Fig. 1). $\beta_{v,h}$ increased with tree age for the three broadleaved species while it seemed invariant for the other ones (Fig. 2). We therefore built a model of $\beta_{v,h}$ for these three species only. The variations of $\gamma_{h,\mathrm{DBH}}$ with tree age were similar to the variations between $\alpha_{v,\mathrm{DBH}}$ and tree age except that no variation was detected for *P. grandidentata* (Fig. 3). As our interest was in general trends, the 5 % highest values were excluded from the analysis.

Then, we tested different growth functions (Chapman-Richards, Gompertz and logistic) and the best of these three models was selected using Akaike's information criterion (AIC). The logistic function gave the models that fitted our data best for all allometric exponents considered and was therefore selected for the future modelling steps, as indicated by Eq. 3:

$$\mathrm{AE}_{ijk} = \frac{a_1}{1 + a_2 \times e^{-a_3 \cdot \mathrm{TA}_{ijk}}} + \varepsilon_{ijk} \tag{3}$$

where AE_{ijk} is the allometric exponent ($\alpha_{v,\mathrm{DBH}}$, $\beta_{v,h}$ or $\gamma_{h,\mathrm{DBH}}$) of the growth year *i* of tree *j* in site *k*, TA_{ijk} is the tree age in the growth year *i* of tree *j* in site *k*, ε_{ijk} is the

Fig. 1 Illustration of typical variation of $\alpha_{v,\text{DBH}}$ (where v is tree volume and DBH diameter at breast height) as a function of tree age for cases with **a** continuous increase until a plateau was reached (example given for *Thuja occidentalis*), and **b** an increase towards a local maximum and then a decrease (example given for *Pinus banksiana*). *Grey line* corresponds to spline smoothing of data
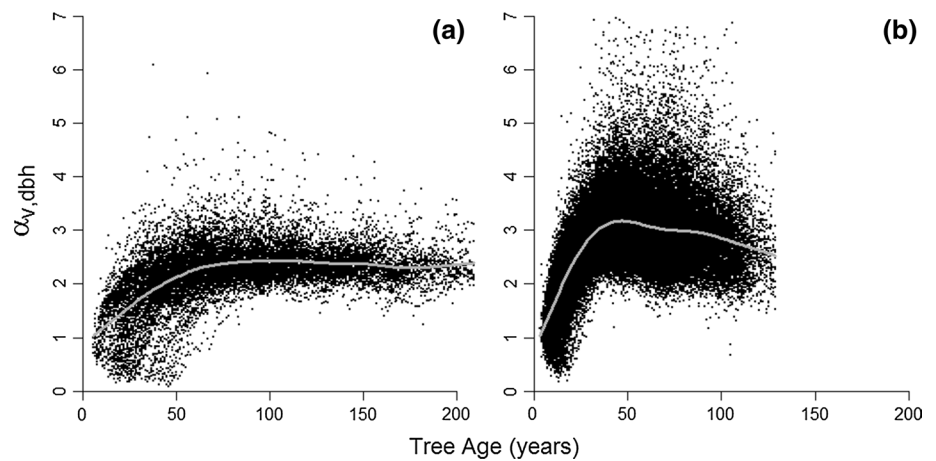

Fig. 2 Illustration of typical variation of $\beta_{v,h}$ (where h is tree height) as a function of tree age for cases with **a** no variation with tree age (example given for *Picea mariana*), and **b** continuous increase (example given for *Populus tremuloides*). *Grey line* corresponds to spline smoothing of data
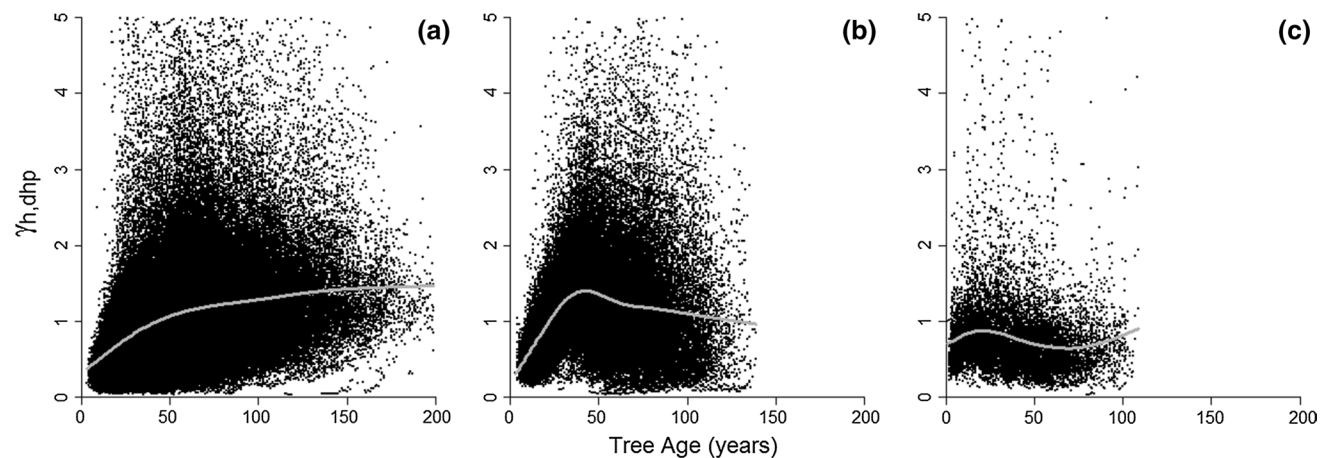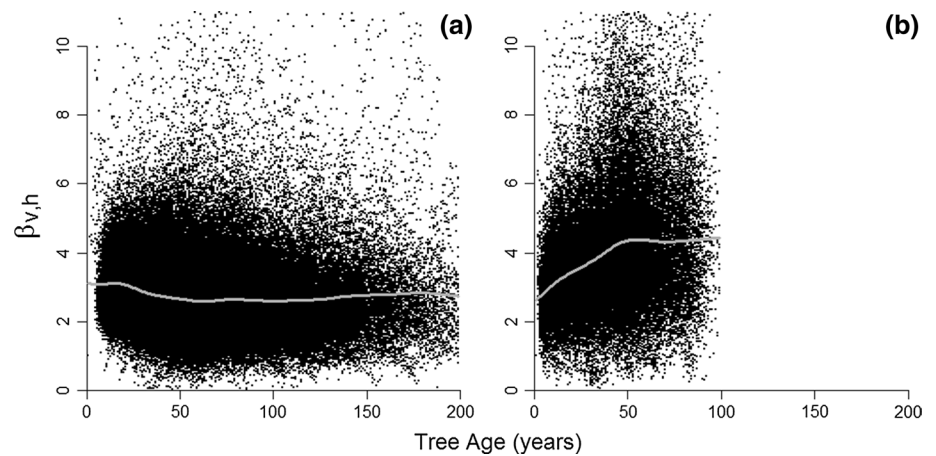

Fig. 3 Illustration of typical variation of $\gamma_{h,\text{DBH}}$ as a function of tree age for cases with **a** continuous increase until a plateau is reached (example given for *Abies balsamea*), **b** an increase towards a local maximum and then decrease (example given for *P. banksiana*), and **c** no variation with tree age (*Populus grandidentata*). *Grey line* corresponds to spline smoothing of data. For abbreviations, see Figs. 1 and 2

residual of the model for the growth year i of tree j in site k [$\varepsilon_{ijk} \sim N(0, \sigma^2)$], and a_1, a_2, a_3 are the parameters of the logistic function.

The following step was to fit the logistic function species by species. We found that the increase of $\alpha_{v,DBH}$ was monotonic for all species except for the two *Pinus* species which exhibited an increase until a local maximum and then an asymptotic decrease. Therefore for these two species, a negative exponential of tree age was additively integrated to Eq. 3 to model the variations of $\alpha_{v,DBH}$ with tree age for *Pinus* species, leading to Eq. 4:

$$\alpha_{v,DBH_{ijk}} = \frac{a_1}{1 + a_2 \times e^{-a_3 \cdot TA_{ijk}}} + e^{-a_4 \cdot TA_{ijk}} + \varepsilon_{ijk} \qquad (4)$$

Similarly, the allometric exponent $\gamma_{h,DBH}$ increased monotonically for all species except for *Populus grandidentata* and *Pinus banksiana*. *P. grandidentata* did not show any variation of $\gamma_{h,DBH}$ with tree age. For *P. banksiana*, $\gamma_{h,DBH}$ increased until a maximum and then decreased without showing any asymptotic behaviour. Therefore, a simple linear function of tree age was integrated additively to Eq. 3, leading to Eq. 5:

$$\gamma_{v,h_{ijk}} = \frac{a_1}{1 + a_2 \times e^{-a_3 \times TA_{ijk}}} + a_4 \times TA_{ijk} + \varepsilon_{ijk} \qquad (5)$$

As data were longitudinal with two hierarchical levels (individuals and sites), we fitted non-linear mixed-effects models using the nlme function of the nlme package (Pinheiro et al. 2007) of the R software (R Development Core Team 2011). Parameters were estimated using the maximum likelihood method and the best model was selected on the basis of AIC comparisons.

By considering both hierarchical levels, random effects on each estimated parameter were tested and the model with the lowest AIC was finally selected. Finally, we tested whether the site and the tree hierarchical levels were significant. The correlation between two successive values of allometric exponents was accounted for by a first-order autocorrelation function (Monserud 1986), which always led to a model with a lower AIC. The homoscedasticity of model residuals and the absence of bias were checked visually.

Influence of shade tolerance on allometric exponents

To characterise the shade tolerance of trees, we used the shade-tolerance index developed by (Humbert et al. 2007) (Table 1). A low index value indicates a shade-tolerant species while a high value of this index indicates a shade-intolerant species. We examined the influence of species shade tolerance on the allometric exponents at two stages of a tree's lifetime: in the juvenile stage (tree age 15 years) and the mature stage (tree age 100 years). For these two tree ages, we used the population mean for each species as predicted by each model constructed (i.e. without considering the random part). For the cases in which no variations of the allometric exponent with tree age were observed, we computed the average species value of the allometric exponent. The estimated allometric exponents for 15- and 100-year-old trees were linearly regressed against shade tolerance.

Results

Average allometric exponents

The average values of $\alpha_{v,DBH}$, $\beta_{v,h}$ and $\gamma_{h,DBH}$ were 2.52, 3.04 and 1.03, respectively, when all species were pooled (Table 1). We also detected a high variability in the allometric exponents as shown by their coefficient of variations, i.e. 29.0, 62.5 and 78.6 %, respectively. In addition, large species-specific differences were observed in allometric coefficients.

Variations of allometric exponents with tree age

From log–log plots, different tree trajectories of volume as a function of DBH or height, or height as a function of DBH, could be identified, where the derivative of the curve corresponds to the allometric exponent. For simplicity, only the plots for *P. rubens* are presented; the other species had similar relationships. The relationships are non-linear (Fig. 4a, c), with a curvature for the smallest DBH, i.e. for the youngest trees. On the contrary, we can see in Fig. 4b that tree trajectories are linear, meaning that $\beta_{v,h}$ is age invariant.

As a general trend, we found that all allometric exponents: (1) either increase toward a plateau, (2) or increase to reach a local maximum and then decrease, (3) or are invariant with tree age (Fig. 4). Our results presented species-specific variations of the allometric exponent's trajectories with tree age. Indeed, the values of the plateaus (parameter a_1, Eq. 3) or the average value of the allometric exponent (when no variation with tree age could be detected) were shown to vary according to the species considered.

Specifically, the values of the plateau for $\alpha_{v,DBH}$ ranged between 2.45 for *T. occidentalis* and 3.12 for *P. rubens* (Table 2). *Pinus* species were particular since the models leading to the best AIC were obtained by adding a negative exponential to the logistic function (Eq. 4). Therefore, the general pattern of variation of $\alpha_{v,DBH}$ with tree age (Fig. 4a) was an initial increase until a local maximum and then an asymptotic decrease towards a fixed value (2.45 and 2.77 for eastern white pine and jack pine, respectively).
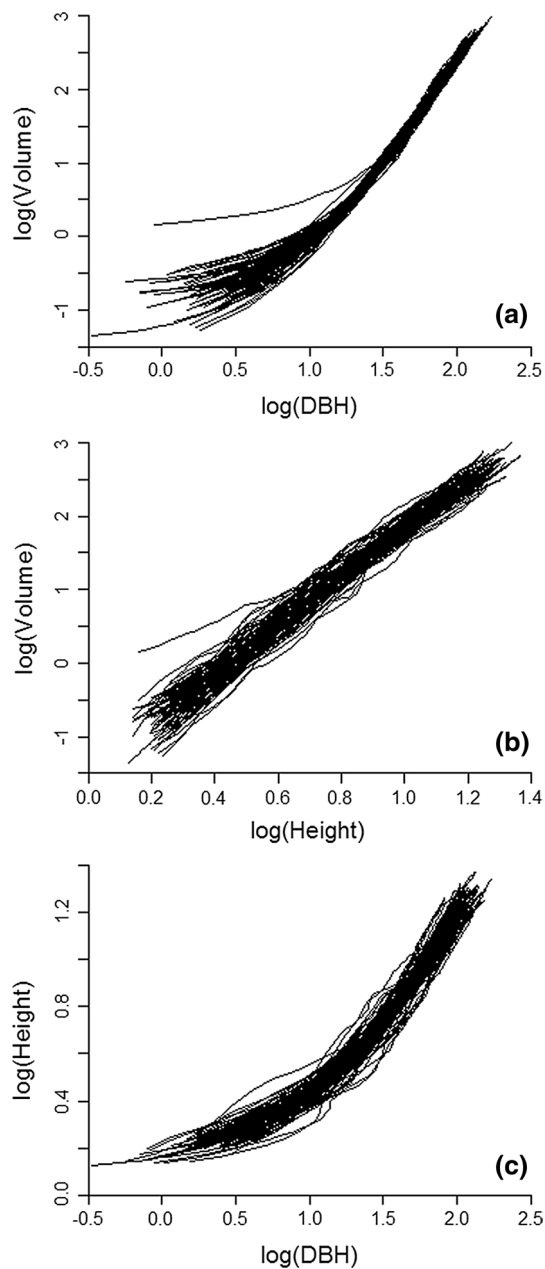
Fig. 4 *Picea rubens* tree trajectories of **a** logarithmic DBH versus logarithmic volume, **b** logarithmic height versus logarithmic volume and **c** logarithmic DBH versus logarithmic height

For the coniferous species, $\beta_{v,h}$ was age invariant, with each species having different $\beta_{v,h}$ averages (Table 1). Broadleaved species showed an increase in $\beta_{v,h}$ with tree age and did not attain their asymptote, except for *B. papyrifera*, during the lifetime covered by the available data (Fig. 4b; Table 3).

The values of the species-specific plateau for $\gamma_{h,DBH}$ varied from 0.874 for *T. occidentalis* to 1.48 for *A. balsamea* (Table 4). *P. grandidentata* $\gamma_{h,DBH}$ was found to be age invariant. The allometric exponent $\gamma_{h,DBH}$ for *P. banksiana*

increased to a local maximum after which it continuously decreased without reaching a plateau.

Model results for $\alpha_{v,DBH}$ and $\gamma_{h,DBH}$ showed that broadleaved species reached their plateau between 30 and 50 years old (Fig. 5). In addition, for old trees, the value of each allometric exponent was found to be similar for *P. grandidentata* and *P. tremuloides* (Tables 2, 3, 4). *P. glauca* and *A. balsamea* reached a plateau for $\alpha_{v,DBH}$ when the trees were older than 50 years. The same trend was observed for the $\gamma_{h,DBH}$ of *P. strobus* and *B. papyrifera*. Finally, *P. mariana* was the species which attained its plateau in $\alpha_{v,DBH}$ the latest (e.g. after 100 years). A similar result was found for $\gamma_{h,DBH}$ of all coniferous species except *Pinus*.

Influence of shade tolerance on allometric exponents

Shade tolerance was found to strongly influence the allometric exponents, and this effect was age dependant (Fig. 6). We demonstrated a significant positive relationship between the index of shade tolerance, the value of $\alpha_{v,DBH}$ and $\gamma_{h,DBH}$ for a 15-year-old tree (p-value <0.001 and = 0.001, respectively). Indeed, $\alpha_{v,DBH}$ varied from 0.58 for shade-tolerant species to 2.52 for shade-intolerant species. $\gamma_{h,DBH}$ increased from 0.24 to 0.79 with increasing shade intolerance of species. $\beta_{v,h}$ for young trees, on the other hand, did not change with shade tolerance (p-value = 0.857).

For old trees, no relationship between the shade tolerance of species and $\alpha_{v,DBH}$ was observed (p-value = 0.860) (Fig. 6). Opposite trends were found when considering $\beta_{v,h}$ and $\gamma_{h,DBH}$. A positive relationship between the index of shade tolerance and $\beta_{v,h}$ was found, since it varied from 2.76 for shade-tolerant species to 5.14 for shade-intolerant species (p-value = 0.031). $\gamma_{h,DBH}$, however, tended to be negatively related to shade tolerance, as it increased from 0.79 and 1.14 with increasing shade tolerance (p-value = 0.066) (Fig. 6).

Discussion

Previous results indicated a high variability in the allometric exponents (Price et al. 2012; Pretzsch and Dieler 2012), but our contribution was not centred on verifying the MST but to establish the variations of $\alpha_{v,DBH}$, $\beta_{v,h}$ and $\gamma_{h,DBH}$ with development stage for a pool of tree species and relate them to shade tolerance. The present contribution therefore evidenced changes of allometry with tree age rather than tree size, as the latter parameter is a consequence of stand density characteristics rather than of development stage (Fig. 5). Such links have not yet been reported. In particular, we showed a strong interaction between development stage and shade tolerance on $\alpha_{v,DBH}$, $\beta_{v,h}$ and $\gamma_{h,DBH}$.

Table 2 Species by species fixed effects of $\alpha_{v,\text{DBH}}$ models using Eq. 3 [all parameters were significant (p-value $<10^{-4}$)]

Species	a_1	a_2	a_3	Autocorrelation	RSE	R^2 (%)
A. balsamea	2.87	29.6	0.184	0.452	0.427	67.8
B. papyrifera	2.75	3.33	0.174	0.257	0.573	35.6
Picea glauca	2.80	3.05	0.0737	0.700	0.525	40.9
Picea mariana	2.84	11.7	0.130	0.510	0.368	70.7
Picea rubens	3.12	7.41	0.110	0.814	0.717	47.1
Pinus banksiana[a]	2.77	16.9	0.166	0.584	0.509	58.0
Pinus strobus[a]	2.45	20.5	0.183	0.801	0.551	39.0
Populus grandidentata	2.69	2.28	0.252	0.348	0.461	31.5
Populus tremuloides	2.78	2.15	0.180	0.387	0.481	39.1
T. occidentalis	2.45	16.1	0.116	0.477	0.311	68.0

RSE Relative SE

[a] Models were fitted using Eq. 4

Table 3 Species by species fixed effects of $\beta_{v,h}$ models using Eq. 3

Species	Mean (SD)	a_1	a_2	a_3	Autocorrelation	RSE	R^2 (%)
A. balsamea[a]	2.89 (1.55)	–	–	–	–	–	–
B. papyrifera	–	3.71	0.743	0.0767	0.838	2.13	13.1
Picea glauca[a]	3.12 (1.67)	–	–	–	–	–	–
Picea mariana[a]	2.76 (1.22)	–	–	–	–	–	–
Picea rubens[a]	3.10 (1.14)	–	–	–	–	–	–
Pinus banksiana[a]	2.98 (1.99)	–	–	–	–	–	–
Pinus strobus[a]	3.26 (1.47)	–	–	–	–	–	–
Populus grandidentata	–	5.16	1.45	0.0577	0.743	2.27	17.4
Populus tremuloides	–	4.96	1.16	0.0522	0.740	1.84	15.8
T. occidentalis[a]	3.46 (1.64)	–	–	–	–	–	–

[a] For these species no development-stage effect in $\beta_{v,h}$ was detectable, and the average $\beta_{v,h}$ with its SD is therefore reported

Table 4 Species by species fixed effects of $\gamma_{h,\text{DBH}}$ models using Eq. 3

Species	Mean (SD)	a_1	a_2	a_3	Correlation	RSE	R^2 (%)
A. balsamea	–	1.48	3.45	0.0465	0.718	0.704	15.7
B. papyrifera	–	1.02	2.64	0.130	0.587	0.597	19.4
Picea glauca	–	1.20	5.78	0.0861	0.618	0.744	12.7
Picea mariana	–	1.36	5.43	0.0631	0.759	0.491	35.0
Picea rubens	–	1.24	5.52	0.0796	0.733	0.513	27.2
Pinus banksiana[b]	–	1.70	7.86	0.124	0.821	0.592	32.4
Pinus strobus	–	1.08	11.1	0.207	0.861	0.544	9.40
Populus grandidentata[a]	0.83 (0.71)	–	–	–	–	–	–
Populus tremuloides	–	0.821	1.40	0.255	0.551	0.571	4.60
T. occidentalis	–	0.874	7.22	0.0733	0.802	0.319	29.0

[a] For this species no development-stage effect in $\gamma_{h,\text{DBH}}$ was detectable, and we report here the average $\gamma_{h,\text{DBH}}$ with its SD

[b] Model was fitted using Eq. 5

Considering our results, we suggest that the MST should include inter- and intra-specific differences in its formulation, not only for the normalisation constant, but also for the allometric exponents.

Variations of allometric exponents with development stage

Previous studies have presented variations with development stage of the allometry between tree biomass and both DBH and h for common beech in Europe (Genet et al. 2011) or between biomass and DBH for a large data set of tree species (Pilli et al. 2006). The effect of development stage on $\alpha_{v,\text{DBH}}$, $\beta_{v,h}$ and $\gamma_{h,\text{DBH}}$ was suggested for three European tree species (Pretzsch et al. 2012). However, our study is the first to establish the variations with development stage of both $\alpha_{v,\text{DBH}}$, $\beta_{v,h}$ and $\gamma_{h,\text{DBH}}$ for a large number of species on a large area and at the inter-annual level.

In accordance with the study of Pretzsch et al. (2012), we found that $\alpha_{v,\text{DBH}}$ and $\beta_{v,h}$ (for broadleaves) increased with increasing tree age. We also showed a positive relationship between $\gamma_{h,\text{DBH}}$ and tree age, while another study showed an inverse relationship (Pretzsch et al. 2012).
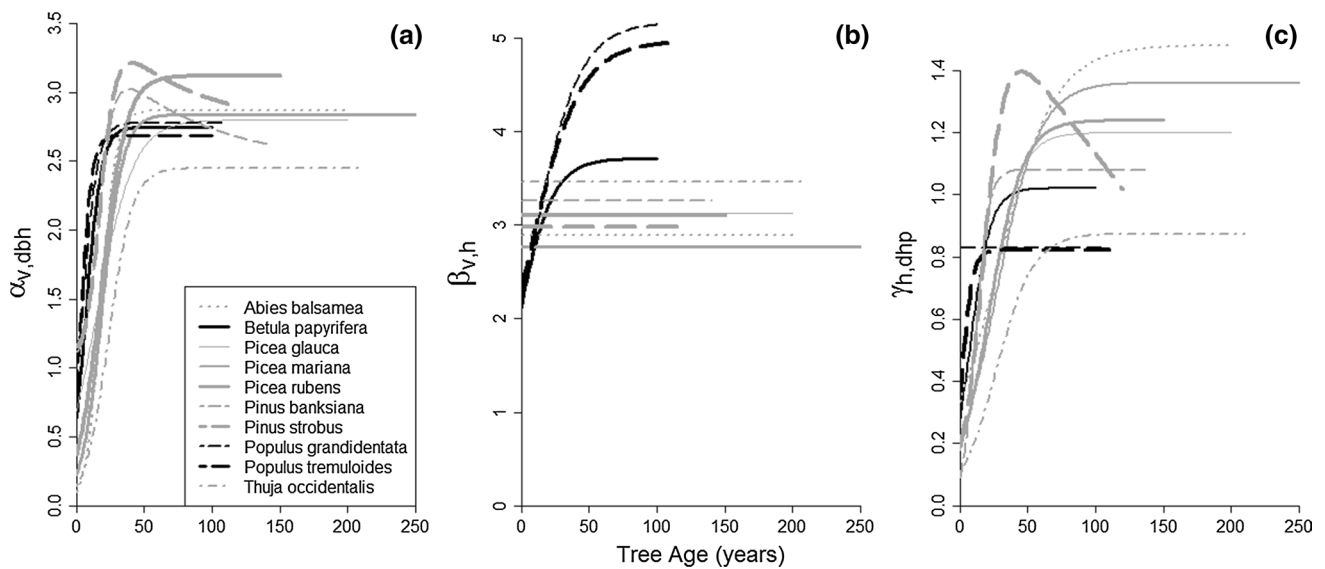
Fig. 5 Effect of development stage on **a** $\alpha_{v,\text{DBH}}$, **b** $\beta_{v,h}$ and **c** $\gamma_{h,\text{DBH}}$ for conifers (*grey lines*) and broadleaved species (*black lines*). For abbreviations, see Figs. 1 and 2
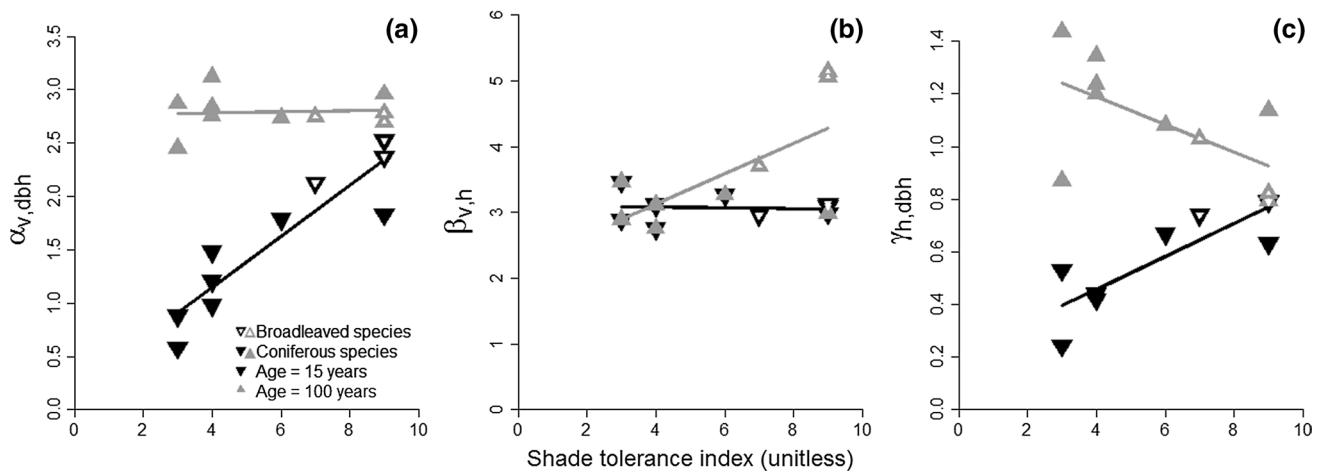

Fig. 6 Influence of shade tolerance on allometric exponents **a** $\alpha_{v,\text{DBH}}$, **b** $\beta_{v,h}$ and **c** $\gamma_{h,\text{db}}$ for trees aged 15 years (*black triangles*) and 100 years (*grey triangles*). *Empty triangles* indicate broadleaved species

However, this latter study considered a static relationship between $\gamma_{h,\text{DBH}}$ and tree age (i.e. without considering inter-annual inter-individual and inter-stand variations), although it has been demonstrated that this static relationship may be erroneous (Henry and Aarssen 1999). Our dynamic approach consisted of a meticulous exploration of the intra-specific, inter-individual and intra-individual variations of $\gamma_{h,\text{DBH}}$. Following a similar scheme a previous study reported an increase of $\gamma_{h,\text{DBH}}$ with tree age (Watt and Kirschbaum 2011), consistent with our findings.

The positive relationships between tree age and $\alpha_{v,\text{DBH}}$, $\beta_{v,h}$ and $\gamma_{h,\text{DBH}}$ were interpreted as an over-investment of tree growth in the crown compared to the stem (Pretzsch

et al. 2012). However, this interpretation is invalidated by previous studies showing that biomass partitioning changed with tree age in order for the tree to allocate relatively more biomass to the stem rather than to the crown for *Pinus strobus* (Peichl and Arain 2007), *Pinus banksiana* and *Picea mariana* (Goudiaby et al. 2013).

Such variations of allometric exponents with development stage could be directly related to the well-known changes in the functionality of wood from the juvenile to the mature stage. Indeed, young trees have to keep stem and branches flexible in order to optimize the search for light (King 1990) and resistance to wind (Bertram 1989). Therefore, it was understandable that a low value of $\alpha_{v,\text{DBH}}$

in the juvenile stage corresponds to a poor investment of trees in diameter compared to height growth.

On the other hand, old trees have to favour the maintenance of the stem: trees have to resist buckling (Niklas 1999) and at the same time wind forces (Lachenbruch et al. 2011). When getting larger, trees also have to face increases in hydraulic constraints, which explains why trees cannot exceed a certain height (Ryan and Yoder 1997). As a consequence, trees invest more in diameter growth, leading to an increase in both $\alpha_{v,DBH}$ and $\gamma_{h,DBH}$. Such an increase is therefore interpreted as the necessity for the tree to invest more in diameter when they grow older in order to maintain mechanical safety and avoid buckling (Niklas 1999). This explains why coniferous species' $\beta_{v,h}$ remain constant throughout their life: their investment in height remains steady as a consequence of their strong apical dominance (Hallé et al. 1978; Millet 2012).

We present evidence that allometric exponents increase and then reach a plateau with age. This may be a direct manifestation of the changes in tree functioning with developmental stage. Indeed, as stated before, the juvenile stage is an expansion phase with strong investment in height and resource acquisition in order for the tree to overcome shading by the neighbouring trees. On the contrary, when trees are maturing, their functioning changes and more resources are allocated to functions which are in competition with the carbon allocated to DBH, height and volume growth. As an example, trees develop their branches in order to maximise their photosynthetic area (Barthelemy and Caraglio 2007) and allocate resources to reproduction through flowering (Bazzaz et al. 1979; Obeso 2002; Thomas 2011). The consequence of this is that trees maintain an equilibrium in their different functional requirements, e.g. between conduction (through height) and mechanical stability (through DBH and volume) but their investment is more limited resulting in a plateau in the allometric exponents with age.

Species-specific variations of allometric exponents

Species to species variations of allometric exponents were expected as this has been demonstrated previously for diverse allometric exponents and when considering many species (Duursma et al. 2010; Pretzsch and Dieler 2012). In addition, we hypothesized that the species to species variation may be explained by differences in a particular functional trait: shade tolerance (Valladares and Niinemets 2008). A previous study proposed rather the use of the wood density of trees to explain the variations of $\gamma_{h,DBH}$ (Ducey 2012). Indeed, this work demonstrated that species with low density had a higher $\gamma_{h,DBH}$ than species with denser wood. However, wood density is known to be positively correlated with shade tolerance (Aiba and Nakashizuka 2009). We therefore decided to explore the

relationships between allometric exponents and shade tolerance rather than wood density as shade tolerance is a better representation of the choice in allocation and growth of species (Givnish 1988).

More importantly, requirements of functional properties change with development stage (Lachenbruch et al. 2011). Therefore it was justified to search for an effect of the interaction between functional traits and development stage for the species to species differences in allometry.

In the juvenile stage, light-demanding species should invest more in height when trees are small in order to overcome the effect of surrounding trees and avoid shading (Givnish 1988; Valladares and Niinemets 2008): stems are slender and crown depth is low (Aiba and Nakashizuka 2009). In addition, it has been shown that saplings of shade-intolerant species grow more steadily in both height and diameter than shade-tolerant species (Ameztegui and Coll 2011; Lilles and Astrup 2012). When trees experienced increasing exposure to light, shade-intolerant saplings were found to compete better than shade-tolerant ones by increasing their relative growth rate (Walters and Reich 2000). Therefore the fact that shade-intolerant species such as *Pinus* or *Populus* exhibited higher $\alpha_{v,DBH}$ and $\gamma_{h,DBH}$ than shade-tolerant species may be explained by a higher investment in height than in DBH during the juvenile stage.

In addition, wood functional requirements during the mature stage are different for trees according to their shade tolerance. Indeed, when considering photosynthetic production, it is known that when trees grow older, late-successional (shade-tolerant) species have a decisive competitive advantage over early successional (shade-intolerant) species (Bazzaz 1979; Valladares 2003; Anderson-Teixeira et al. 2013). Shade-tolerant species are also able to benefit from an increase in light intensity following an opening of the canopy. Therefore, in the mature stage, these species will have stronger height growth rate than shade-intolerant species (Canham 1988; Henry and Aarssen 1997). This explains why $\gamma_{h,DBH}$ and $\beta_{v,h}$ were, respectively, negative and positive with the shade-tolerance index. Specifically this signifies that shade-tolerant species can increase their height growth investment in a mature forest in order to benefit from an opening of the canopy. However, this conclusion should be moderated for $\beta_{v,h}$ since this allometric exponent did not present any variation with tree age for coniferous species.

Implication for the MST

From its theoretical basis, the MST predicted that the values of the allometric exponents should have been: $\alpha_{v,DBH} = 8/3$, $\beta_{v,h} = 4$ and $\gamma_{h,DBH} = 2/3$ (West et al. 1999, 2009). In our study, we considered both static (Table 1) and dynamic (Fig. 4) situations. From these results we could

not confirm the predictions of the MST, in accordance with previous findings on European tree species for the same allometric exponents (Pretzsch et al. 2012; Pretzsch and Dieler 2012).

The MST is based on organism structure and functionality from the cell to the ecosystem scale (Brown et al. 2004). The normalisation constant (*b*; Eq. 1) is known to vary according to the kind and size of the organism considered (Gillooly et al. 2001), but also, for woody species, between angiosperm and gymnosperm (Enquist et al. 2007) as well as species by species. However, this theory does not account for competition ("distributions of abundances among coexisting species of similar size") or for the requirements of plants to grow (Brown et al. 2004). Only a few studies considered specific and development-stage variations of the scaling exponent (Pretzsch and Dieler 2012). We demonstrated that, in addition to these sources of variations, the MST would benefit from a consideration of the influence of some functional traits on the scaling exponent.

A Boltzmann function was integrated into the MST to represent how the metabolic rate of trees is modulated by temperature (Gillooly et al. 2001). Our work highlights the possibility of improving the theoretical framework of the MST by integrating some processes suggested by functional traits. Shade tolerance represents how species intercept light and how efficiently the intercepted light is converted into photosynthates (Henry and Aarssen 1997). These processes are already taken into account in the MST. However, this functional trait also accounts for the resource allocation in the different tree compartments (Givnish 1988; Henry and Aarssen 1997) and for the use of the available environmental resources in order to allow competition for them (Reich et al. 2003). To date, such a phenomenon is not taken into account in the MST.

Previous studies have proposed inclusion of the notion of limiting resources in the MST by considering the allometry between individual mass and density of trees growing under the self-thinning law (Lin et al. 2012, 2013). They achieved this by adding two terms representing abiotic stress (e.g. water availability) (Maestre et al. 2009), and competition symmetry (Schwinning and Weiner 1998). In the light of our results, a species-specific parameter for age dependency must also be considered. In other words, the functional requirements (i.e. the resources needed) are species specific and have to change with development stage. In order to better assess this new framework, further studies are required in order to better establish the specific variations in functional requirements with development stage and competition symmetry. Future work should be to translate these empirical variations into a mathematical formulation and integrate it into the MST.

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